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OBSERVATIONS AND EXPERIMENTS ON THE LIFE HISTORY OF THE SALAMANDER, *DESMOGNATHUS FUSCUS FUSCUS* (RAFINESQUE)

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The common Dusky Salamander, *Desmognathus fuscus fuscus*, is one of the best known of American salamanders. Its life history, thanks to the studies of several investigators, especially Wilder (1913, 1917), has been worked out in considerable detail. Dunn (1926) has reviewed the literature and summarized the features of especial interest to naturalists. Since Dunn's monograph appeared, several contributions have been made to the life history of this salamander. A different interpretation of the color pattern formation has been made (Noble, 1927), the spermatophore has been described in detail, and the distinctive features of the spermatozoön analyzed (Noble and Weber, 1929). Most phases of the courtship have been witnessed (Noble and Brady, 1930) and the courtship of the closely related *D. quadra-maculatus* observed in full detail (Noble, 1931). Since spermatophores of *D. f. fuscus* have been found in fall, spring, and summer, the courting season is apparently very extended. The hatching of the eggs is not due to "sufficient friction" of the enclosed embryo as Wilder (1913) assumed but to the digestive action of a series of unicellular glands scattered over the embryo's snout (Noble and Brady, in press). The present paper represents a continuation of these studies. It includes an analysis of the brooding habit, the larval life, and the habitat selection of the adult.

It is well known that the eggs of *D. f. fuscus* are laid on land and are guarded by the mother. Wilder (1917) has made detailed observations on the brooding habit and has found that a brooding female will guard the eggs of another individual. When a female that had been brooding eggs until the time of hatching was introduced into the "nest" of another female she assumed an unusual pose: "instead of lying among them with her body coiled about them, she stood over them with her body elevated so that the eggs were beneath the belly and only slightly in contact with them . . . . she was invariably found in the same peculiar attitude with relation to the eggs, and always with the head oriented in the same direction."

This unusual pose was the same as that which the rightful owner of the eggs had assumed when brooding them. Wilder (p. 16) comments on this situation in part:

"Of course there is no means for determining whether the actual finding of the eggs by the foster mother was a reaction to the proximity of the eggs themselves, or was a purely accidental occurrence, since *Desmognathus* frequently seeks out positions under stones and other objects lying upon the surface. . . . The peculiar position and orientation of the bodies of the two females while successively brooding this particular batch of eggs is most satisfactorily explained, however, as a response to some unusual conditions in the surroundings of the nest, such as the possible entrance of a little light into the nest from one direction."

Since Wilder's conclusions were based upon a single experiment it seemed to us desirable to secure additional data on the brooding poses of *D. f. fuscus*. It also seemed desirable to perform additional experiments in exchanging the eggs before accepting the conclusion that females will adopt the eggs of other females. By means of the pituitary technique it is possible to secure the eggs of a large number of females at one time. We have induced sixteen females to lay their eggs in the laboratory by implanting the anterior pituitaries of a series of *Rana pipiens* under the skin of their throats. The salamanders were maintained in separate crystallizing dishes provided with damp sand, moss, and frequently some small sticks or stones added to serve as additional cover. The eggs when brooded usually developed normally in these dishes.

Our observations on the fourteen females that laid eggs and began to brood them showed conclusively that no one pose is assumed during brooding to the exclusion of all others. When returning to the egg-mass after being removed from it the female usually lowers her head and thrusts her head and shoulders under or between the eggs (Noble, 1931a, Fig. 136). However, she may partly coil about the eggs. Most of the eggs in our series were laid under the moss in such a position that they could not be examined without the risk of disturbing the female. One female in the series laid her eggs against the side of the dish and we were able to make observations on her behavior during brooding without lifting the moss. The female, No. 6 in our series, laid on April 23 after receiving three implants of frog anterior pituitary. A summary of our record follows:

The eggs were laid in a single cluster hanging from some moss in contact with the glass side of the dish. From April 23 to 27 the female was frequently observed. Sometimes she remained beneath the eggs

with her head bent at a sharp angle to her body and thrust up among the eggs. In this position the throat of the female was in contact with the glass and the top of her head with the eggs. At other times she was flat on the bottom of the dish with her head facing outward and directly below the eggs. On May 1, the female was found to have assumed a third position. She was lying on her back with her head bent at an angle to her body and the top of her head against the side of the dish. On May 2, the female had pushed up into the cluster of eggs while keeping her back to the side of the dish. In this position the weight of her body was supported in part by the bent tail. On May 4, she had moved to a position below the eggs and lay between sand and moss. On May 5, she was in the same position.

In 1913, Wilder wrote (p. 262) "I have no evidence that the habit of eating the eggs, such as Smith ('07) found in the case of *Cryptobranchus*, is ever indulged in by *Desmognathus*, although, as will be shown below, this species is by no means to be exempted from the charge of cannibalism."

Among the sixteen females that were induced to breed in our laboratory we have proved that two devoured most of their own eggs. In neither case had the brooding habit been fully established before the destruction of the eggs began. In the first case a female laid her eggs April 20 in the usual two clusters but these were deposited in two different places in the dish. By April 23, no brooding habit had been established. By May 4, the eggs appeared to be reduced in number and a supply of enchytræids was added as a source of food. Nevertheless, by the following day, only three eggs were left. These were developing normally. The enchytræids had widely spread over the dish. On May 6, the female was killed and thirteen eggs were found in her stomach. No mature eggs were in the ovary.

The second case of egg eating occurred in specimen No. 8, which was induced to lay by implanting two frog anterior pituitaries on May 6 and two *Gyrinophilus* pituitaries on May 8. The eggs were laid May 11, but the female did not brood the eggs on the following day. Her body held against the side of the glass gave evidence of her having eaten a few eggs. The eggs were therefore removed to one of the upper layers of moss. This dish was examined on May 14, 23, 25 and 26, but the female was never seen with the eggs. By June 1, only three eggs were left. The others could be readily seen distending the stomach of the female. On June 4, the three eggs still remained. These were preserved as well as the female. An autopsy revealed that she had laid all the mature

eggs in her ovary. This was done apparently before eating any of those laid.

In order to determine whether the female was interested in her eggs more than in the protected retreat where they were laid we have performed a series of experiments. The experiment with salamander No. 10 may be considered typical of this series. The salamander laid her eggs June 15, after four implants of frog pituitary. She coiled about them and began at once to brood. On June 16, the female was driven from her burrow and the eggs removed to a new hollow on the opposite side of the dish. On June 17, the female was not seen to brood the eggs and on the 18th the eggs were moved back to the original hollow to which the female had returned. No brooding was observed until June 22, when the female was found in contact with her eggs throughout the day. At 5 P.M. the eggs were removed to the opposite side of the dish and seven artificial eggs constructed out of paraffin coated with gelatin and agreeing closely with the original eggs in size were placed with the female. She remained in contact with these artificial eggs throughout the 23d until she was driven from her burrow late in the day. On the 24th the female had returned and was in contact with the artificial eggs. She was driven from the burrow and was not seen in it the next day. During this period she did not brood her eggs which had been removed to a little burrow in the moss on the other side of the dish. On July 1, the artificial eggs were removed and the female's eggs were returned to their original location in the burrow where they were laid. The next day the female was back in the burrow and brooding the eggs. On July 3, the eggs were removed again a short distance from the original burrow and some artificial eggs constructed of agar jelly were placed in the original site of egg-laying. On July 6, the female was back in the burrow and lying among the lumps of agar which had lost much of their original resemblance to eggs. On July 7, 8 and 9 she was not in the burrow or near her eggs. On the 10th she had found her eggs and was brooding them. It was apparent from these experiments that a female *D. f. fuscus* will brood artificial eggs if these are placed in the original site of egg-laying. She will apparently return to the original burrow in preference to hunting for her eggs placed a few centimeters away.

If a brooding female is shifted into another crystallizing dish containing an unprotected cluster of eggs she will usually lose little time in finding and brooding these foreign eggs. For example, salamander No. 10, discussed above, was shifted to dish No. 14 on July 13 and the next day was found with head thrust among the eggs in the usual brooding

posture. On the same day, she was transferred to dish 15 and was found close to these eggs the following day. On July 16, she was also apparently brooding the eggs but left them when the cover of moss was lifted. She was shifted the same day to dish 17 and was found brooding these eggs on July 23. On that day she was placed back in her own dish where she continued to brood her eggs until July 31, when some of them hatched.

We have introduced the eggs of other species of Amphibia into the breeding dishes of *Desmognathus* and have also tested the reactions of the brooding female to damp objects. Our experiments with salamander No. 1 may be considered representative of this type of experiment. The salamander laid her eggs March 23 after receiving three implants of frog anterior pituitary. She coiled about them at once and did not move when the stone covering the eggs was lifted. On March 31, at 3:30 P.M. the eggs were removed to the opposite side of the dish and a mass of moist filter paper was placed under the stone in the position previously occupied by the eggs. By 5 P.M. the same day, the female had found the eggs and was brooding them. Here was a case where the female was much more attracted by her eggs than by her nesting site.

The experiment was carried further by transferring the female to a foreign breeding dish. The dish selected, No. 2 in our series, contained a brooding female which had been particularly attentive to her eggs. She had laid fifteen eggs on March 21 and thirteen more on March 23, thus breaking the rule of laying her eggs in one night. She was driven from her eggs at 3 P.M., March 31, but had returned to them by the following morning. The eggs had been laid in two clumps, one near the edge of the dish and the other in the center. There was a well-marked burrow between the two sets of eggs. The female was usually to be found with her tail in contact with the more scattered group in the center of the dish under a stone, and her head directed toward the other group of eggs. On one occasion she was found in exactly the opposite orientation. When salamander No. 1 was introduced into this dish on April 2, she did not brood either set of eggs that day. On April 4, she was brooding one lot and not trying to brood both as in the case of the rightful owner.

The salamander was next returned to her original dish (No. 1) and the eggs were placed in another part of the dish. By April 6, she had found the eggs and was lying with head thrust among the eggs even though these were at a distance from the original egg-laying site. On April 8 at 10 A.M. the female was still brooding these eggs. She was driven away and the eggs were returned to the original site of laying on the opposite side of the dish. A clump of wet paper towel was placed in the

hollow where the female had been brooding for at least two days. By 9:30 A.M. the next morning she had found the eggs and was brooding them. The eggs were then removed to the far side of the dish and replaced by fifteen well-developed eggs of *Ambystoma opacum.* These had been laid the previous fall and kept in good condition in an ice box. They were washed before being placed in the *Desmognathus* "nest." By 1:30 that afternoon the female had found her eggs in the new position and was brooding them. At that time the *Desmognathus* eggs were moved to a new spot, the *A. opacum* eggs were placed where the *Desmognathus* eggs had been, and some eggs of *Eurycea bislineata cirrigera* were placed in the position formerly occupied by *A. opacum* eggs. At 10:30 the following morning the female was found in contact with the *A. opacum* eggs. At 3:30 P.M. the female still had her head thrust among the *A. opacum* eggs. Some of the eggs had begun to hatch. The lot was then moved to the position of the *E. b. cirrigera* eggs and these were moved to a new position. Although there was now the possibility of brooding the eggs of three different kinds, no brooding was observed again. The *E. b. cirrigera* eggs molded and were removed, April 13. The unbrooded *Desmognathus* eggs remained in good condition and the embryos could be seen moving within the egg capsules on April 20.

It appeared to us quite possible that the female was not brooding the *A. opacum* eggs, but was merely lying with head thrust among them waiting for the young to hatch, whereupon she would devour them. Noble and Brady (in press) have shown that *D. f. fuscus* in nature will devour the eggs of *A. opacum.*

A series of experiments was devised using eggs constructed out of agar jelly, or masses of gelatine to attract the brooding *Desmognathus.* The females in general showed little interest in these artifacts. Their indifference stood in striking contrast to their response to their own eggs. Our experiments with salamander No. 14 may be considered typical of the series. The female laid her eggs June 18, after receiving five implants of frog anterior pituitary. The salamander brooded her eggs until June 24, when they were moved to another part of the dish without disturbing the female. The salamander was not seen brooding until June 29, when it was apparent that she had moved most of her eggs to a position near the center of the dish. On July 1, the cluster of eggs was moved back to the side of the dish where a few scattered eggs indicated the spot from whence they had been removed by the female. The next day the female was found in the center of the dish. Since the female showed no disposition to find her eggs, a mass of cold gelatine about the size of her egg-

mass was placed near the female in the center of the dish. The female did not come in contact with this gelatine that day or the next. In the afternoon of July 3, several small pieces of jellied agar were placed directly on the top of the female's head. On July 6, the female had found the eggs on the side of the dish and was brooding them. The eggs were moved back to the center of the dish and some new masses of jellied agar having the form of eggs were placed in the position occupied by the eggs. The next day the female had found her eggs in the middle of the dish and was brooding them. She remained in contact with them from July 7 to 13.

Our most extensive series of experiments was directed toward establishing the reaction of the female toward eggs of another female of the same species. The ease with which a female introduced into a foreign dish would find the eggs and the persistency with which she would brood them showed conclusively that the brooding female is attracted by eggs of its own species whether or not she laid them herself. In thirteen transfers of a brooding female to a foreign dish examined twenty-four hours later, the female was found to be brooding the foreign eggs eight times. For example, salamander No. 14 was transferred on July 13 to the dish of No. 10. The next day she was brooding the eggs with head thrust among the cluster. On that day she was transferred to dish No. 17. Apparently she brooded the eggs from July 15 to 17, when she was transferred again to dish No. 10. On July 23, she was found brooding the eggs and was transferred to dish No. 21. On July 30, apparently she was brooding the eggs of this female while her own eggs left in dish No. 14 were hatching. We use the word "apparently" above because in some cases, when the moss was lifted for purposes of observation, the female would withdraw slightly from the eggs. Although actual contact with the eggs was not observed at every examination, there can be no doubt that a brooding female exhibits considerable alacrity at finding the unprotected eggs of another female and will usually be found brooding them within twenty-four hours after being released in an unfamiliar dish containing the eggs.

In contrast to the above results, all of our cases of a female's apparent brooding of artificial eggs could be accounted for by assuming that the female tends to return to the location where she laid her eggs. If artificial eggs are placed in this position she may appear to brood them. We found no instance of a female's brooding artificial eggs in a nest made by the experimenter, although living *Desmognathus* eggs would attract a female to these locations. Our artificial eggs were constructed of gelatin,

of agar jelly, of moist paper towel, and of paraffin as described above, and they were placed in a wide variety of situations without calling forth the brooding response.

On August 28, 1930, one of us collected near Mt. Storm, West Virginia, a set of eggs of *Desmognathus fuscus fuscus* which had just hatched. On the same day near Table Rock, in extreme western Maryland, another set of eggs of the same species was secured just before hatching. The first lot of eggs was in a shallow mud basin under a rock, the second was on some rotting wood under a stump. Water flowed only 12 cm. from the first set while the second was near the edge of a damp stream bed. The latter nesting site was unusual in that the stream bed apparently had been made by rain-water and the permanent stream was several yards away. The recently hatched young of the first lot were placed in a tin container half full of damp moss, and were brought back to New York alive.

Early in September the contents of the container were transferred to a crystallizing dish 20 cm. in diameter and a supply of enchytræids added. On October 23, the young salamanders appeared to be in good condition. Six were removed to a similar crystallizing dish containing water approximately 2 cm. in depth. Six others were allowed to remain in the other crystallizing dish which contained damp moss but no free water on the bottom of the dish. White worms were again added to both dishes as a source of food. Both lots of young lived, and by March 5, 1931, it was found that some of those in the dish of damp moss had completely metamorphosed, while none in the water showed evidence of this change. We had found that *Desmognathus fuscus fuscus* was able to pass through its larval stages on land without having access to free water. Under these conditions metamorphosis occurred earlier than if the larvæ enjoyed a larval life in the water.

The larvæ reared in the damp moss invariably remained darker than those in the water, and this may have been due to the fact that the moss tended to screen them from the light.

Their gills were shorter and they did not grow as rapidly as the aquatic larvæ. The most striking difference between the larvæ was in the length and shape of the tail. Those reared in the moss had shorter tails in proportion to their body-lengths than those reared in water. Further, they lacked any evidence of the tail-fin which characterizes the aquatic larvæ. An average specimen of the lot reared on damp moss and preserved March 9 measures 15 mm. from tip of snout to cloaca, and 25 mm. in total length. An average specimen of the larva reared in

water on the same day measures 16 mm. from snout to cloaca and 30 mm. in total length.

By April 23, the aquatic larvæ had fully metamorphosed. One of the larvæ reared in moss was still incompletely metamorphosed. The temperature in the laboratory apparently had speeded up the development of the aquatic larvæ above the rate found in nature and doubtless also influenced the developmental rate of the terrestrial larvæ as well. The terrestrial habitat seemed to have hastened metamorphosis in some but not in all of the larvæ reared under moss. An average specimen of this lot reared under damp moss and preserved in formalin April 23 measures 15 mm. from snout to cloaca and 25.5 mm. in total length. In striking contrast, an average specimen of the lot reared in water measures 16 mm. from snout to cloaca and 31.5 mm. in total length. Therefore, the latter has a slightly larger body and a decidedly longer tail.

We have repeated the experiment with two additional sets of *D. f. fuscus* eggs. We secured both sets in March by implanting the anterior pituitary gland of frogs into female salamanders that happened to have spermatophores protruding from their cloacæ. Both salamanders had completed laying by March 23. Although both sets of eggs were kept on water-tables, one set began hatching May 9, and all in the set had hatched by May 16. The second set did not begin hatching until June 6, but all the eggs had hatched by June 15.

The recently hatched larvæ of the first set of eggs were divided into two lots. On May 18, one lot was placed in a crystallizing dish 20 cm. in diameter containing water 1 to 1.5 cm. in depth. The second was placed on wet sand in a crystallizing dish of the same size and covered with damp moss. A plentiful supply of enchytræids was added to both dishes and the latter were placed near each other on a table over which tap-water flowed continuously. At intervals, larvæ from both lots were preserved in formalin. On July 1, approximately forty-six days after hatching, some of the larvæ reared under the damp moss shed their skins in one or more large pieces. This shedding is considered definite evidence of metamorphosis in caducibranch salamanders. These larvæ had cut their usual larval period of about nine months to about one and one-half months. However, this shortening of the larval period was due not only to the enforced aërial respiration but also to the high temperatures that occurred during these months.

The second set of eggs was treated similarly to the first. They were divided into two lots on June 6. Seven of the eggs which had not hatched

by this day were placed in water. By June 8, they had hatched and the larvæ seemed very much at home in the water and made no attempt to crawl up the sides of the glass. Again, larvæ from both lots were preserved at frequent intervals. By July 10, when the experiment was discontinued, neither lot of this second set showed any evidence of metamorphosis.

In both sets the larvæ reared on wet sand under damp moss grew more slowly than those reared in the water. This may have been due to difficulties of feeding in the terrestrial habitat. These larvæ reared under moss also agree in lacking a tail-fin and in having decidedly shorter tails in proportion to their body-length than the larvæ reared in the water. In the first set of eggs a consistent difference in size between the terrestrial and aquatic larvæ began to appear by June 8. In the second set this difference appeared by June 15. By July 1, a terrestrial larva of the first set measured 11 mm. from snout to cloaca, and 19 mm. in total length. The same day an aquatic larva of this set measured 14 mm. from snout to cloaca and 24.5 mm. in total length. In the second set a terrestrial larva on July 10 measured 11 and 18.2 mm. and an aquatic larva 13 and 23 mm. for the same parts.

The tails of the terrestrial larvæ compared with their total length are proportionately shorter than the tails of larvæ of the same age reared in water. However, the terrestrial conditions have not acted directly upon the tail, stunting its growth. A comparison of the series of larvæ reared on damp sand with the series reared in water shows conclusively that the entire growth of the former series has been checked. The terrestrial larva preserved July 10 is a trifle shorter than an aquatic larva preserved June 15. The apparent stunting of the tail in the older terrestrial larva is due to the fact that the entire growth of the larva has been checked in the terrestrial situation.

At the time of hatching, June 8, the larva measured 9.5 mm. from snout to cloaca and 15 mm. in total length. The increase of 4 mm. in total length which took place in the wet sand habitat during the following month may have been accomplished merely by the absorption of the yolk. However, the young salamander which was preserved April 23, after being reared under wet moss since the preceding October 23, reached a total length of 23 mm. Although its snout was essentially larval in structure, food was contained in the stomach. Unidentifiable fragments of food were also found in the stomachs of the terrestrial larvæ which had metamorphosed by this time and had reached a total length of 25.5 mm. Therefore, it seems highly probable that some food is

eaten by the larvæ when forced to live out of water under damp moss. These larvæ, however, do not attain the size of their brothers or sisters reared in the water.

Although Wilder (1913) was the first to give a detailed description of disproportionate growth of the tail in the larvæ of *D. f. fuscus* we are unable to accept the interpretation she has given to this datum. She states (p. 277):

"The increase in length of the tail is the principal factor in the change in length proportions of the body. These changes in the tail are obviously a preparation for aquatic life which is soon to follow."

We find this more rapid growth of the tail a phenomenon common to many salamanders. It occurs in *Batrachoseps attenuatus* and *Aneides æneus*, which pass their entire life on land and consequently never use the tail as a swimming organ. In fact, Mrs. Wilder has shown that a similar rapid growth in the tail of *D. f. fuscus* occurs also at the time of metamorphosis, when the salamander is preparing itself for what is essentially a terrestrial life. She states (p. 294) in regard to the larva:

". . . the average proportions and size of the body remain practically the same until late spring, when there occurs a marked increase in the average size and a decided change in the proportionate lengths of the regions of the body in that the tail lengthens more rapidly than either the head or trunk."

Wilder compares the development of *D. f. fuscus* with that of *Eurycea bislineata*. The eggs of the latter species are aquatic, poorly provided with yolk, and the larva consequently escapes from the egg-capsules in a more juvenile condition than does *D. f. fuscus*. Wilder assumes that in *D. f. fuscus*, at the time of hatching, the longer hind legs are "undoubtedly accounted for by the demands of this short terrestrial period preceding the aquatic larval life." It may be noted, however, that all Amphibia well provided with yolk tend to hatch in a more mature condition than those poorly provided with this substance. The well-developed condition of *Cryptobranchus* at hatching is not an adaptation to terrestrial life which it never experiences. Similarly the well-developed limbs of *D. f. fuscus* may be looked upon primarily as a consequence of an ample endowment of yolk. Wilder (1913, p. 273) comments further:

"While the limits of the terrestrial larval stage are somewhat indefinite, the structural changes which take place during this period are very important."

For the reasons stated above we are unable to accept the changes in proportion as an adaptation to terrestrial life. Unlike the terrestrial

larvæ of various Salientia such as *Hoplophryne* and *Sooglossus*, the larvæ of *D. f. fuscus*, during their stay on land, show no structural change in the branchial region other than a reduction in length of the gills. Wilder describes the early development of granular glands in the integument as an adaptation to exposure to air. In *Ascaphus*, also, granular glands develop early and the tadpoles of this species are prone to work their way out of water apparently while feeding (Noble and Putnam, 1931). In spite of this possible terrestrial adaptation in *D. f. fuscus*, the terrestrial larva remains primarily adapted for aquatic life.

Wilder (1917, p. 17) remarks "That the terrestrial larval stage is really a definite one is shown by the behavior of the newly hatched larvæ when placed in water . . . they will not remain in the water, but persistently crawl out and lie, often in a mass together, in the moist debris along the edges. It is not until all external evidence of the yolk mass has disappeared that they will remain in the water."

We have found that eggs ready to hatch may be placed in water and the larvæ will emerge normally. From the moment of hatching, our larvæ, as stated above, seemed fully adjusted to the water and made no effort to escape from the dishes. In view of the fact that the eggs of *Desmognathus* are often placed only a few centimeters from the edge of the stream where they would be caught by the rising waters following a heavy rain, it seems highly probable that in nature *D. f. fuscus* must frequently take up at once a larval life in the water. Conversely, other experiments reported above have shown that if the stream bed remains moist but devoid of free water the larva may pass its entire premetamorphic life on land. In brief, our experiments show that the life history of *D. f. fuscus* is more plastic than Wilder assumed on the basis of her observations.

Wilder (1917, p. 18), discussing her two sets of *D. f. fuscus* eggs, remarks: "The period of incubation in both these broods was approximately eight weeks (53–55 days in the first case and 56–57 days in the second), a considerably longer time than that previously estimated by me, which was five weeks."

One set of eggs that was laid in our laboratory April 17 hatched on June 6 to 8. This gives an incubation period of fifty to fifty-two days. But five sets of eggs that were laid June 15, 18, and 22 hatched practically together on July 30 or 31. Probably the laboratory temperatures were higher than those to which the eggs would be subjected near their native brooks. It is apparent that the temperature considerably influences the period of incubation in *D. f. fuscus*.

Wilder (1913) assumed that the mode of life history of *D. f. fuscus* has played an important part in controlling the distribution of the adult. She states (p. 256):

"The element of close proximity to running water in the habitat of *Desmognathus* is certainly not necessary to the immediate physiological demands of the adult, but is incident rather to the aquatic nature of the larval life, which makes necessary not only easy access to water after hatching, but also requires that the supply of water shall be perennial, since each year the newly hatched larvæ reach the water at about the time when the brood of the previous summer leave the water as very small adults."

However, there are various salamanders such as *Ambystoma maculatum* and *Hemidactylium scutatum* that lay eggs in or near the water and yet find it congenial to live at considerable distances from water throughout most of the year. We have presented evidence above that streams are not necessary for the larval life of *D. f. fuscus*. It seems to us that the stream habitat of *D. f. fuscus* is a consequence of adult requirements. In this connection the field observations of one of us appear to be pertinent. It is well known that *D. f. carolinensis* differs from the typical form in its tendency to move away from the stream beds. Although the eggs are laid near streams in the manner of *D. f. fuscus*, the adults may be found shortly after the breeding season at considerable distances from water. They are found under logs in the woods, associated with the various species of *Plethodon*. From August 21 to 28 one of us was collecting in Virginia, western Maryland, and West Virginia. The season was dry and most of the *Desmognathus* were near the streams. Occasionally a specimen of *D. f. carolinensis* and one of *D. f. fuscus* would be found together under the same stone, but this was not the rule. The great majority of the several hundred *D. f. carolinensis* taken were found on damp ground at a distance from the stream-beds, while the *D. f. fuscus* were close to the running water. This difference of habitat selection was particularly noticeable at night when, with the aid of electric hand-lamps, both species could be seen wandering about, each tending to keep to its own territory. A particularly favorable spot for demonstrating this habitat difference was the road of Route 50 running west for two miles from Table Rock Inn. The road cuts a series of small streams that seep from the bank along the south side of the road. Here, on two evenings, many *D. f. carolinensis* were seen wandering over the wet stones of the steep bank while the *D. f. fuscus* were at the foot of the bank where the seepage tended to form a stream. While the latter

situation was wetter than the former, it seemed to us that there were mechanical factors that also tended to keep *D. f. fuscus* in its habitat. *D. f. carolinensis* was very agile in running over these wet, vertical surfaces. On the night of August 28, an adult *D. f. fuscus* was seen trying to climb up a vertical bank along the road beyond Table Rock Inn. After climbing about 20 cm. it slipped and fell. It rested about two minutes and tried the climb again. This time it succeeded and slowly worked its way up the vertical bank. When it was approximately half-way up the salamander was touched lightly on the tail. Instead of wriggling off rapidly over the surface of the wall in the manner of *D. f. carolinensis* it fell heavily to the bottom of the bank again. Only on one other occasion was another *D. f. fuscus* seen sticking to this vertical bank. The typical form is heavier than *D. f. carolinensis* and possibly for this reason alone it is unable to work its way rapidly over vertical surfaces. However, very few *D. f. carolinensis* were found in the stream-beds with *D. f. fuscus.* Apparently *D. f. carolinensis* selects damp ground in preference to the immediate vicinity of streams. There is still another reason for habitat segregation: *D. f. fuscus* usually escapes danger by plunging into the stream, while *D. f. carolinensis* when stimulated tends to run rapidly away, seeking for a crevice in which to hide. In brief, apparently there are several factors which tend to isolate these two closely related subspecies during adult life. The mode of life history has played little or no part in this isolation.

D. f. fuscus and *D. f. carolinensis* occur together over a wide area of Virginia, western Maryland, and West Virginia, without intergrading. The ability of *D. f. carolinensis* to live in damp soils at a distance from flowing water has given it a much wider local range than *D. f. fuscus* enjoys. This was clearly brought to the attention of one of us while carrying on field work in this area. For example, near the top of Spruce Knob in West Virginia, at an altitude of 4860 feet, only *D. f. carolinensis* was found on August 26 and 27, 1930. The form was abundant in damp ravines through which mountain streams flowed during most of the year. In the open fields several hundred feet below the top of the mountain there is some seepage from springs. Here, under rocks, another series of *D. f. carolinensis* was taken, but no *D. f. fuscus.* Back Run Creek lies in a valley along the southern edge of the mountain. When this creek was reached, *D. f. fuscus* and *D. phoca* began to appear. Under stones two or three feet from the water approximately 90 per cent of the *Desmognathus* caught were *D. f. carolinensis.* *D. fuscus* was taken in considerable numbers under stones lying on the edge of the stream. *D.*

phoca was caught by turning over the larger stones in the same situation. In this region where *D. quadra-maculatus* does not occur, *D. phoca* was living in the same habitat as *D. f. fuscus* but, in correlation with its larger size, was frequenting larger crannies below the rocks along the edge of the stream. Only once were a *D. phoca* and a *D. f. carolinensis* taken together under the same rock a few centimeters from the water. *D. f. fuscus* and *D. phoca* being of different sizes were living successfully together in the same stream-beds. *D. f. carolinensis* is smaller than *D. f. fuscus* but it avoids competition chiefly by selecting moist ground at a distance from water.

In North Carolina where the large and powerful *D. quadra-maculatus* may come into the picture there is, in certain localities at least, a restriction of adult *D. phoca* to the muddier streams (Noble, 1927). We have found in the laboratory that *D. quadra-maculatus* feeds readily on any small specimens of *Desmognathus*. It has been our custom to keep this species in good health by feeding it on these salamanders alone. On the other hand the cannibalistic habit is not common in the other species, and we have found it advisable to feed them on earthworms. It would be interesting to determine by field experiments how large a part the cannibalistic habit of *D. quadra-maculatus* has played in the disappearance of adult *D. phoca* from certain streams where the former species is abundant.

CONCLUSIONS

1.—The larval life of *Desmognathus fuscus fuscus* is more plastic than has been hitherto assumed.

a. A terrestrial stage may be omitted. Eggs will hatch in water and the larvæ will live from the time of hatching in this medium without endeavoring to escape.

b. An aquatic larval stage may be omitted. Larvæ have been reared from hatching to metamorphosis, in dishes provided merely with damp moss.

2.—Larvæ of *D. f. fuscus* reared under damp moss do not attain the size of their brothers or sisters reared in the water.

3.—A brooding female is attracted by the eggs of its own species and will find and brood the eggs of another female when these are placed in dishes unfamiliar to the salamander.

4.—A brooding female tends to return to the site of egg laying. It will brood artificial eggs placed in this site but not those placed elsewhere in the dishes.

5.—Females which have laid eggs but failed to brood them may later eat these eggs.

6.—*D. f. fuscus* and *D. f. carolinensis* occur together in part of western Virginia, western Maryland, and West Virginia. They avoid competition by selecting different habitats. Their different climbing abilities and their different avoiding reactions, also, tend to keep them apart.

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